

REVIEW OF FOSSIL HALIOTIDAE (GASTROPODA) FROM NEW ZEALAND WITH DESCRIPTION OF A NEW EARLY MIOCENE SPECIES

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Abstract. Subgenera of *Haliotis* to which the Recent species are assigned are used in this review of the New Zealand fossil fauna. *H. matihetihensis* and *H. australis* are assigned to *Padollus*, and *H. virginea* and *H. flemingi* to *Paua*. A new species, *Haliotis (Marinauris) hokiangaensis* n. sp., is described from the early Miocene Otaua Group, Matihetihe, west Hokianga, Northland. Ten New Zealand fossil *Haliotis* species are allocated to six subgenera with few apparent lineages. Six New Zealand fossil haliotids are older than those presently known as fossils from Australia. The apparent incidence of New Zealand Cenozoic haliotids possessing shell characteristics of later Australian and South African taxa may be a result of convergent evolution in a local environment, but more likely a radiation eastwards from New Zealand in the late Oligocene onwards, when the circum-Antarctic Current began to flow. DNA inference in Recent New Zealand *Haliotis* suggests the possibility that in the late Palaeogene-early Neogene, New Zealand haliotids were a result of local radiation from either ancestral Tethyan or Panthalassian Ocean progenitors.

KEYWORDS: Haliotidae; Gastropoda; *Euhaliotis*; *Marinauris*; *Notohaliotis*; *Padollus*; *Paua*; *Sulculus*; new taxon; early Miocene; Pliocene; Otaian; New Zealand.

INTRODUCTION

Recent haliotids (Gastropoda: Haliotidae), commonly known as paua or abalone, are a commercial mollusc taken wild or aqua-cultivated for meat, pearl, and shell. Their economic value, environmental considerations, and fecundity have motivated research (e.g. Minh 1999). They are not common fossils, and research on fossil haliotids worldwide has been sporadic (e.g. Talmadge 1963, Dauphin *et al.* 1989, Pickery 1991, Lee & Vacquier 1995, Geiger 1999), with occasional overviews (e.g. Lindberg 1992, Geiger 1998a, Geiger & Groves 1999). There are isolated records of New Zealand fossil haliotids (e.g. Harris 1897, Suter 1913, Powell & Bartrum 1929, Fleming 1952, Carter 1972, Lee *et al.* 1983), with descriptions of New Zealand fossil haliotids being published by Powell (1938), Fleming (1952), Beu *et al.* (1990), and Eagle (1996, 1999).

Fossil record numbers are those of the New Zealand Fossil Record File and are prefixed by the appropriate NZMS 260 1: 50,000 map designation (e.g. R09). New Zealand fossil *Haliotis* types are held in the collections of Auckland War Memorial Museum (AK) and the Institute of Geological and Nuclear Sciences, Lower Hutt (GS). A possible new species of haliotid is held by the Geology Department, University of Otago (OU).

TAXONOMY

DNA research confirms the Haliotidae to be monophyletic (Lee & Vacquier 1995, Geiger 1999). As with most fossils, specimen preservation affects identification of haliotid taxa. The fragile, aragonitic, auriform haliotid shells are often shattered by strong currents and wave action, especially given the hard bottom, high-energy environment in which they live. Rocky shore facies and their fossils are rarely preserved because of this high-energy regime (Beu *et al.* 1990, Eagle *et al.* 1995, Eagle 1999). A poor fossil record results (Powell 1938, Beu *et al.* 1990, Eagle 1999). Haliotids usually delaminate or are crushed during sediment deposition and compaction (Eagle 1999), or (particularly in middle Cenozoic or older specimens) may be preserved as internal/external moulds with no or only partial shell details. Populations of Recent haliotid species are morphologically variable, and fossil populations probably also were (Geiger & Groves 1999).

In extant *Haliotis* species, shell characteristics can be modified by ontogeny, environmental controls, or hybridisation. Epipodia (Owen *et al.* 1971) and radulae (Herbert 1990) have been used for additional character sets in Recent species, but these are lost in fossils. Whereas sound taxonomy results from the availability of many specimens in the Recent, most New Zealand fossil haliotids are described from one specimen (e.g. Powell 1938, Fleming 1952). Recent haliotids have been classified by biological means, such as inferences from cDNA sequences of sperm lysin (e.g. Lee & Vacquier 1992, 1995; Geiger 1999). Nomenclature in this paper follows that of Knight *et al.* (1960), Beu *et al.* (1990), Eagle (1996, 1999) and Geiger & Groves (1999).

SYSTEMATICS

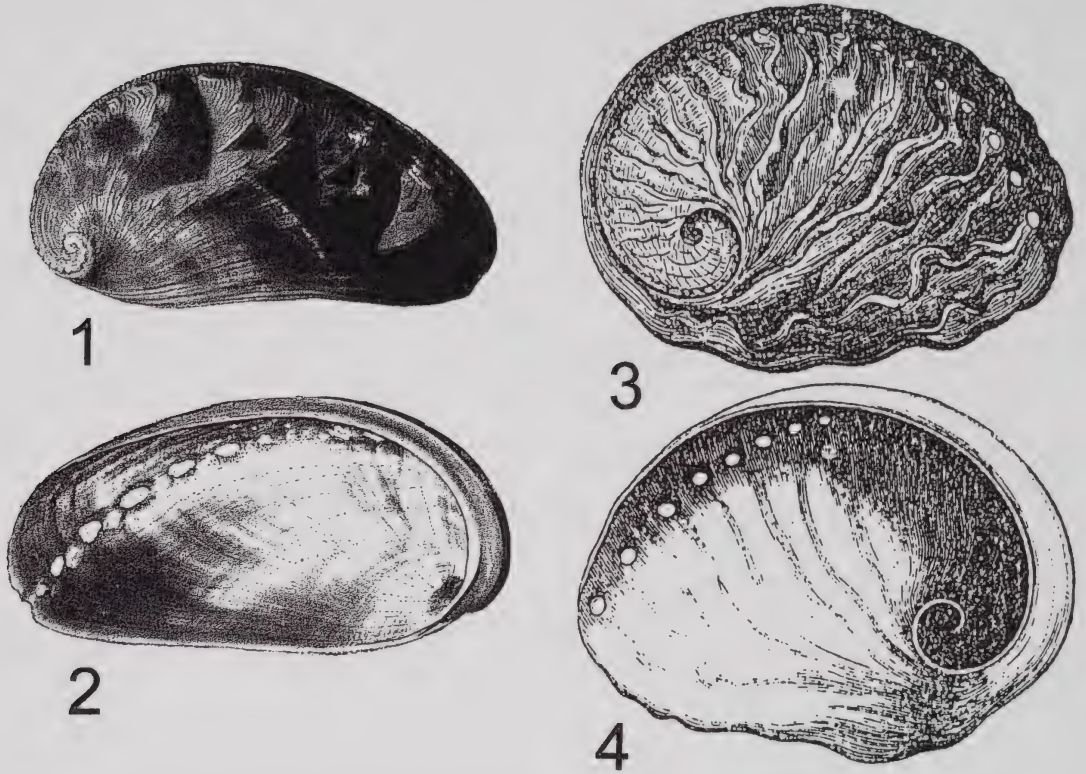
CLASS:	GASTROPODA Cuvier, 1797
SUBCLASS:	ORTHOGASTROPODA Ponder & Lindberg, 1996
SUPERORDER:	VETIGASTROPODA Salvini-Plawen, 1980
ORDER:	ARCHAEOGASTROPODA Thiele, 1925
SUBORDER:	PLEUROMARIINA Cox & Knight, 1960
SUPERFAMILY:	PLEUROTOMARIACEA Swainson, 1840
FAMILY:	HALIOTIDAE Rafinesque, 1815
GENUS:	<i>Haliotis</i> Linnaeus, 1758
Type species:	<i>Haliotis asinina</i> Linnaeus, 1758 (by subsequent designation, Denys de Monfort, 1810, Conch. Syst. 2, p.119, under L'Haliotide; Recent, Indo-Pacific).

RANGE

Late Cretaceous (Maastrichtian) – Recent.

DIAGNOSIS

Shell auriform, asymmetrical, with low or raised spire situated more or less off-centre or sub-centre posteriorly; columella forming a wide flat or concave ramp around left side joining basal lip, sometimes with flange; spiral row of closed and open exhalant respiratory tremata along left side; no operculum.



Figs 1–4. 1–2. Recent *Haliotis* (*Haliotis*) *asinina*. Length 100 mm. 1. Dorsal. 2. Ventral. 3–4. Recent *Haliotis* (*Padollus*) *midae* (after Van Nostrand 1956). Length 95 mm. 3. Dorsal. 4. Ventral.

COMMENTS

Knight *et al.* (1960) recognised 11 subgenera in *Haliotis*; 13 subgenera were recognised by Vaught (1989). However, these have been significantly reduced in number among Recent species as a result of DNA research (Hara & Fujio 1992, Brown 1993, Lee & Vacquier 1995). The shell of *Haliotis asinina* (Figs 1, 2) is elongate and narrow, with an eccentric apex. Being an atypical species, no other species are assignable to the nominate subgenus.

SUBGENUS: *Euhaliotis* Wenz, 1938

Type species: *Haliotis midae* Linnaeus, 1758 (by original description; = *elavior* Pilsbry, 1890; *capensis* Dunker, 1841). Recent, South Africa, South America.

New Zealand species: *H. mathesonensis* Eagle, 1996.

DIAGNOSIS

See Eagle (1996).

COMMENTS

H. (Euhaliotis) mathesonensis Eagle, 1996 is very large (diameter 170 mm; width 141 mm). The South African Pleistocene to Recent *H. (Padollus; emend Lee & Vacquier 1995) midae*

(Figs 3, 4) is morphologically the most similar haliotid to *H. (E.) mathesonensis*. *H. (P.) midae* is distinguished from *H. (E.) mathesonensis* by corrugations running obliquely to those of the growth lines, by being more ovate than elongate-ovate and by having a low spiral apex situated sub-centrally a quarter of the way along the specimen. For palaeo-ecology see Eagle *et al.* (1999).

Haliotis (Euhaliotis) mathesonensis Eagle, 1996

See Eagle (1996) for the description and illustrations of this Early Otaian (Burdigalian) fossil from the Cape Rodney Formation at Matheson's Bay, north Auckland. The holotype (AK72925) is the only specimen known.

DESCRIPTION

See Eagle (1996).

SUBGENUS: *Marinauris* Iredale, 1927

Type species: *Marinauris melculus* Iredale, 1927 (by subsequent designation, Wenz, 1938). Recent, Indo-Pacific, Queensland.

New Zealand species: *H. hokiangaensis* n. sp.

DIAGNOSIS

See Eagle (1999).

COMMENTS

Haliotis (Marinauris) melculus (Iredale, 1927) (Fig. 5) was synonymised with *H. (M.) brazieri* (Geiger 1998b) (Fig. 6). *H. (M.) brazieri* is ovate with an elevated spire. The upper surface of *H. (M.) brazieri* has a raised central spiral area and the sutural ramp is sculptured with numerous narrow, flat-topped, spiral ribs of irregular size, crossed by sharp, crescentic, transverse ridges with transverse striae in the interspaces. The tremata are large and oval, on slightly elevated tubercles, and normally six are open. *H. (M.) brazieri* has latera with a sharp-edged peripheral rib, concave below with about six roughly nodulose ribs. The shell is small (4 cm) compared with most haliotids.



Figs 5–6. 5. Recent *Haliotis (Marinauris) melculus*. Length 7 mm. Dorsal. 6. Recent *Haliotis (Marinauris) brazieri*. Length 30 mm. Dorsal.

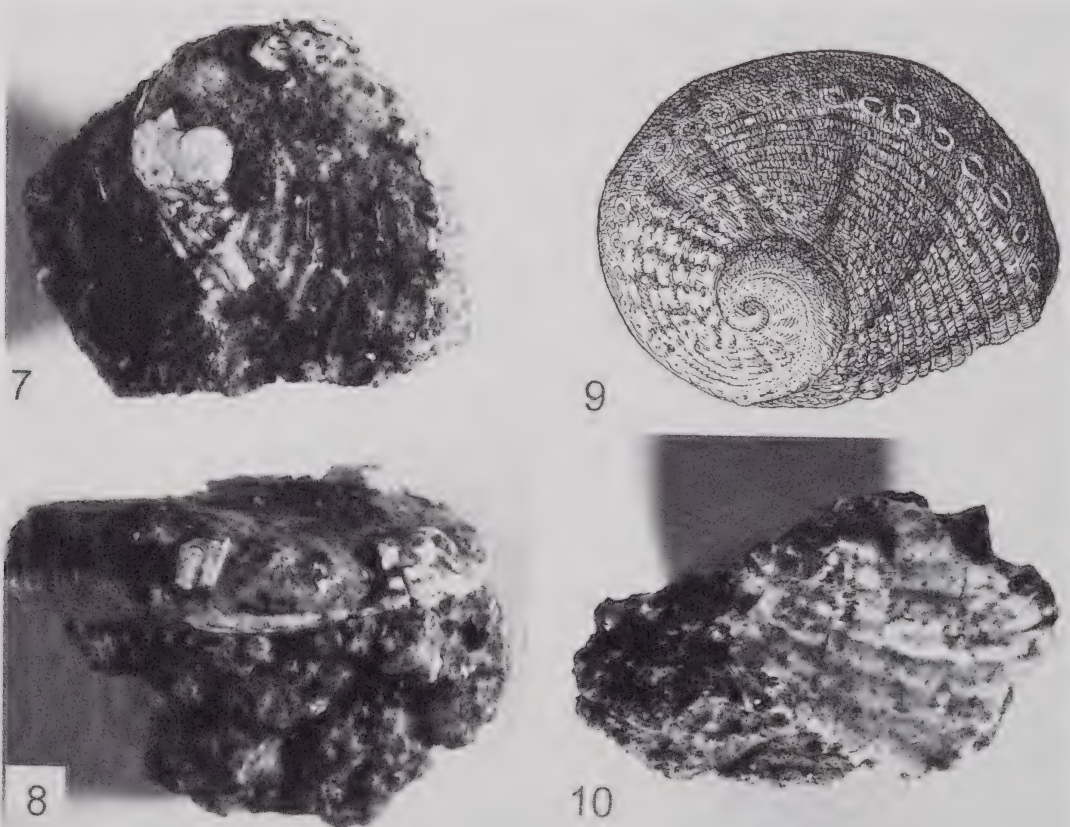
Haliotis (Marinauris) hokiangaensis n. sp.
(Figs 7–10)

MATERIAL

Holotype. AK73252; specimen filled with sandstone matrix with parts of shell separated from steinkern; portion of apertural lip missing.

TYPE LOCALITY

Waititi Formation (Ballance *et al.* 1978), Otaua Group, O05/f143 grid reference O05/367403; cutting on south side of Matihetihe Road opposite Tangata Whenua Marae, adjacent to the Maori cemetery, near beach access, Matihetihe, north-west Hokianga, Northland. The fossil locality (Fig. 11) is part of a highly fossiliferous volcanoclastic mass flow deposit, now eroded to an isolated remnant. Irregular bands of siltstone (10–15 mm thick) and sandstone (30–50 mm thick) contain occasional carbonaceous fragments and shell hash. The interbedded sandstone contains a mixture of whole and partial (mostly decalcified) molluscs, solitary corals, and annelids.



Figs 7–10. Digital images and schematic reconstruction of the holotype of *Haliotis (Marinauris) hokiangaensis* n. sp. (AK73252). Length 17.6 mm. 7. Dorsal. 8. Anterior. 9. Reconstruction. 10. Shell interior showing radial cord arrangement on a portion of the sutural ramp.

AGE

Otaian (Aquitanian), Early Miocene (Ballance *et al.* 1978).

ETYMOLOGY

Named after the geographical area of Hokianga.

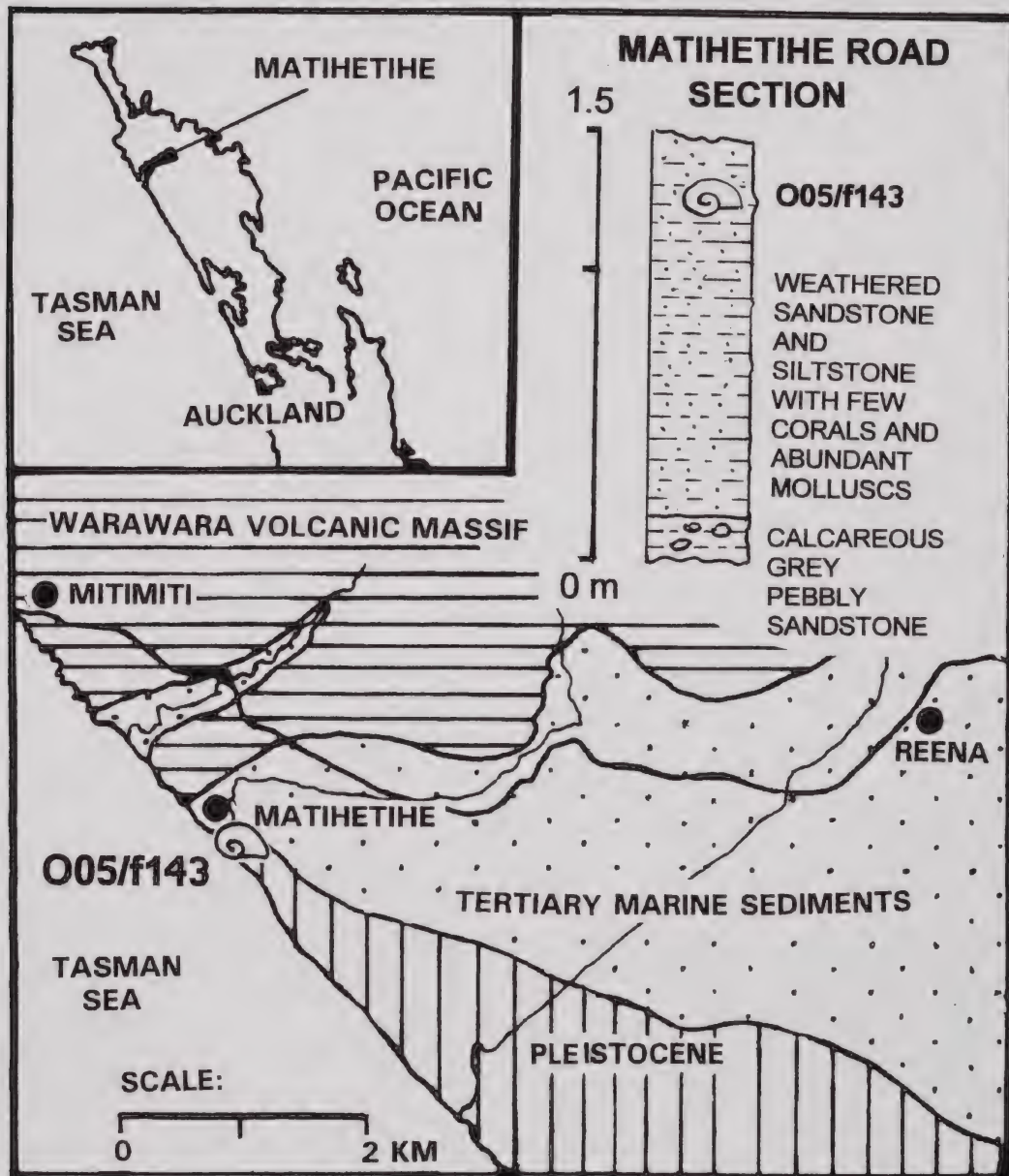


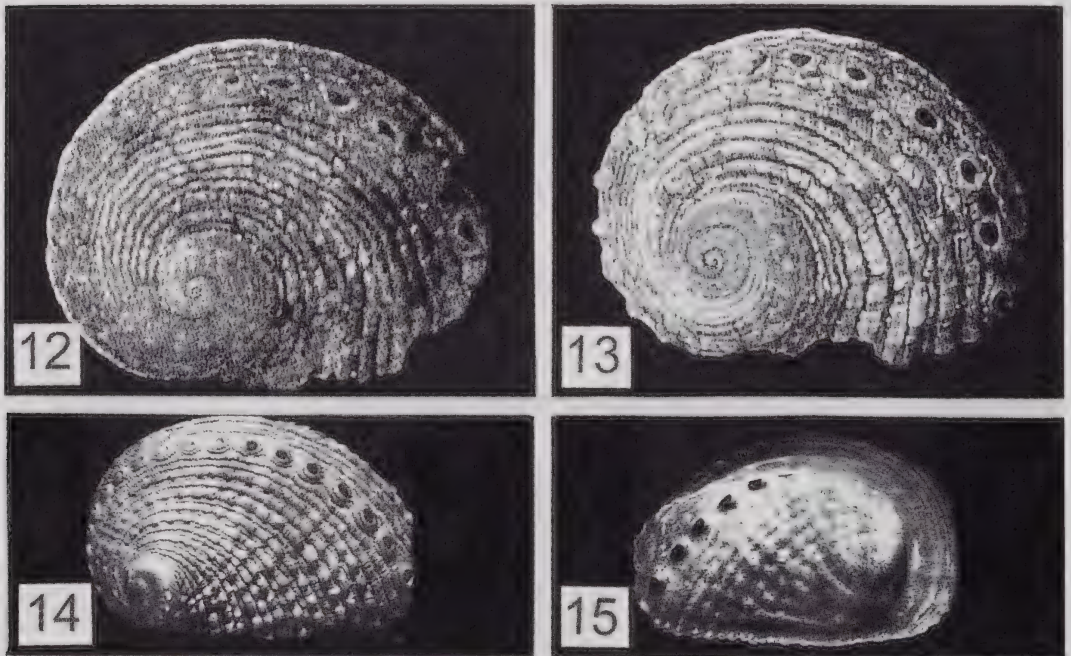
Fig. 11. Location map and stratigraphic column of the Matihetihe road cutting, Northland, New Zealand, showing details of the early Miocene fossil type locality O05/f143.

DESCRIPTION

Shell small, roundly ovate; conspicuous posterior spire, elevated above sutural ramp whorl; teleconch of $1\frac{1}{2}$ whorls, broad, almost flat, last whorl within submarginal apex; spire apex not strongly eccentric; protoconch rounded; dorsal shell spiral ornament with nine strong, subequal, smooth, rounded cords; spiral cords transversely nodulose, crossed by very fine striae, and with shallow, rounded grooves between; narrow irregular radial growth folds; tremata low, conical, small, subcircular orifices with thick, rounded borders; at least four tremata open, 21 on last whorl separating upper whorl surface from outer face; outer face convex with three thick, sharp, unequal spiral cords with deep, narrow, correspondingly unequal grooves; central cord forming a subdued medial keel; anterior lip, labial area unknown. DIMENSIONS: Diameter 17.6 mm, width 11.8 mm, height 4.1 mm.

REMARKS

The small shell size suggests a juvenile, although species in this subgenus do tend to be small. The ovate-circular shell outline, flattened sutural ramp with slightly elevated subcentral spire, sculpture of well-developed spiral cords with axial folds, and low, conical tremata, confirm assignment of *Haliotis hokiangaensis* to the subgenus *Marinauris*. Because part of the penultimate whorl and apertural lip are missing, comparison cannot be made with other species on the basis of the number of open tremata. The most similar in shell morphology to *Haliotis* (*M.*) *hokiangaensis* are the species *H. (M.) ethologus* Iredale, 1927 (Fig. 12); *H. (M.) hargravesi* Cox, 1869 (Fig. 13); *H. (M.) brazieri* Angas, 1869 (Fig. 6); *H. (Sanhaliotis) crebrisculpta* Sowerby,



Figs 12–15. 12. Recent *Haliotis* (*Marinauris*) *ethologus*. Length 7 mm. Dorsal. 13. Recent *Haliotis* (*Marinauris*) *hargravesi*. Length 31 mm. Dorsal. 14–15. Lectotype of Recent *Haliotis* (*Sanhaliotis*) *crebrisculpta* (from Geiger 1998b). Length 30 mm. 14. Dorsal. 15. Ventral.

1914 (Figs 14, 15); *H. (Padollus) roei* Gray, 1827 (subgenus emended Lee & Vacquier 1995) (Figs 16, 17); and *H. (M.) queketti* E. A. Smith, 1910 (Fig. 18).

Geiger (1998a) suggested that *H. (M.) ethologus* from southern Queensland is actually a northern Australian form of the more southern species *H. hargravesi*, and that *H. melculus*, similarly, is the southern *H. brazieri*. He comments that *H. hargravesi* shows extensive intraspecific variations, and that intergrades (i.e. potential hybrids) between these variations and *H. brazieri* exist where the ranges of the two species overlap. The four nominal species are collectively regarded by Geiger (1998a) as the '*hargravesi-brazieri* continuum'.

Stewart & Geiger (1999) ascertained that the three syntypes of *H. crebrisculpta* Sowerby, 1914 were of two different species. One is clearly the shell figured by Sowerby in his original description and is designated by Stewart & Geiger (1999) as the lectotype of *H. crebrisculpta*; the other two specimens are identical with the type of *H. (Sulculus) clathrata* Reeve, 1846 distributed widely in the western Pacific but not considered similar enough for comparison with *H. (M.) hokiangaensis*.

H. (M.) hokiangaensis differs from the small (4 cm) Recent southern Queensland and northern New South Wales species *H. (M.) hargravesi* by having only nine instead of 11 evenly spaced transversely nodulose spiral ribs that are elevated and broadly rounded, not narrow and flat-topped as in *H. (M.) hargravesi*. Although the outer sides of *H. (M.) hokiangaensis* and *H. (M.) hargravesi* are both convex, *H. (M.) hokiangaensis* has only three thick, sharp, unequal radial cords, whereas *H. (M.) hargravesi* possesses four equal radial cords. The small (3 cm) southern Queensland to New South Wales species *H. (M.) brazieri* is more circular than *H. (M.) hokiangaensis* and on the sutural ramp has a broad, smooth central spiral rib bordered by a few incised spiral lines either side, instead of the nine evenly-spaced, broadly rounded, transversely nodulose spiral ribs of *H. (M.) hokiangaensis*. *H. (M.) hokiangaensis* also differs from *H. (M.) brazieri* in having, on the outer side of the shell, three thick, sharp, unequal radial cords, not the three faint ribs in the upper area, and three angular ribs on the bottom showing on the outer shell side of *H. (M.) brazieri*.

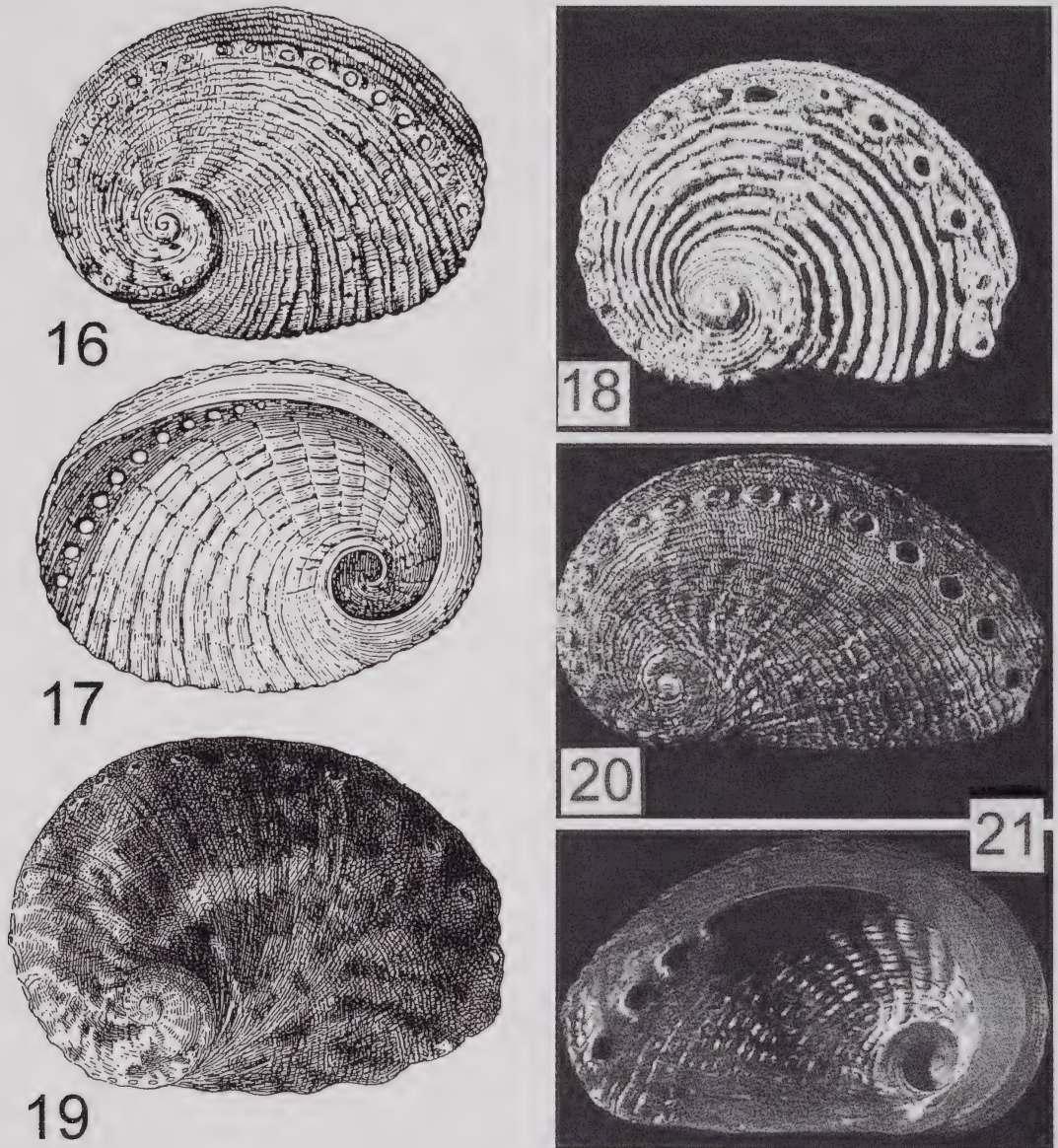
Recent *H. (Sanhaliotis) crebrisculpta*, known only from New Caledonia, differs from *H. (M.) hokiangaensis* by being more elongate-ovate, having 17 rounded and transversely nodulose unequal spiral cords, and an outer side with five sharp cords instead of the three of *H. (M.) hokiangaensis*. The Recent medium-sized (12 cm) Western Australian species *H. (Padollus) roei* differs from *H. (M.) hokiangaensis* in having 14 knotted, rough spiral cords of variable width also crossed by prominent growth folds and a slightly higher spire. Unlike *H. (M.) hokiangaensis*, the rare South African Recent species *H. (M.) queketti* has seven equal, rounded spiral cords on the sutural ramp, tremata with round apertures and thicker borders, and only two sharply defined spiral ribs of equal thickness on outer side of shell.

The conspicuous spire posteriorly elevated above the sutural ramp whorl, the broad, almost flat, last whorl within submarginal apex, the dorsal spiral ornament of nine strong, equal, smooth transversely nodulose rounded cords, crossed by very fine striae with shallow rounded grooves between, and the outer concave face with three thick, sharp, unequal radial cords (the central cord forming a subdued medial keel), differentiate *H. (M.) hokiangaensis* from other fossil or Recent haliotids.

SUBGENUS: *Notohaliotis* Cotton & Godfrey, 1933

Type species: *Haliotis naevosa* Martyn, 1784 (by original designation; not binomial; = *ruber* Leach (Fig. 11), 1814; *tubifera* Lamarck, 1822; *gigantea* Peron, 1816). Australia.

New Zealand species: *Haliotis* sp.; *H. waitemataensis* Powell, 1938.



Figs 16–21. 16–17. Recent *Haliotis (Marinauris) roei* (after Van Nostrand 1956). Length 81 mm. 16. Dorsal. 17. Ventral. 18. Dorsal view of Recent *Haliotis (Marinauris) queketti*. Length 29 mm. 19. Dorsal view of Recent *Haliotis (Padollus) ruber* (from MacPherson & Gabriel 1962). Length 79 mm. 20–21. Recent *Haliotis (Notohaliotis) clathrata* (from Geiger 1998b). Length 29 mm. 20. Dorsal. 21. Ventral.

DIAGNOSIS

Tremata on tubular projections situated on angulation separating upper whorl surface from flat or concave outer face; ornament spiral cords, threads crossed by irregular transverse ribs oblique to collabral lines (Knight *et al.* 1960). No raised or prominent dorsal rib.

COMMENTS

Recent *Haliotis* (*Padollus*) *ruber* Leach, 1814 (subgenus emended Lee & Vacquier 1995) (Fig. 19), from New South Wales to South Australia and Tasmania, is ovate with a rounded dorsal surface and a low spire; it has broad radial folds crossed by many fine, beaded spiral cords on the sutural ramp, and 6–7 open tremata of conical tubercles with a spiral concave area between these and the margin. *H.* (*Notohaliotis*) *clathrata* Reeve, 1846 (Figs 20, 21) “. . . from Queensland has a small, depressed, almost circular shell and may be a variant of *H.* (*P.*) *ruber* . . .” (Wilson *et al.* 1993: 50).

***Haliotis* (*Notohaliotis*) *waitemataensis* Powell, 1938**

(Figs 22, 23)

TYPE LOCALITY

Bostaquet Member, Cape Rodney Formation, Kawau Subgroup (Hayward & Brook 1984), basal Waitemata Group (Ballance 1974), Akarana Supergroup (Ballance *et al.* 1978); in sandy limestone, Fossil Point, east side of Bostaquet Bay, Kawau Island.



Figs 22–24. 22–23. Holotype of *Haliotis* (*Notohaliotis*) *waitemataensis* (AK72068). Length 56 mm. 22. Dorsal. 23. Posterior. 24. Dorsal view of *Haliotis* (*Padollus*) *scalaris emmae* (from MacPherson & Gabriel 1962). Length 58 mm.



MATERIAL

Holotype. AK72068, complete specimen with some adherent matrix.

AGE

Early Otaian (Burgidalian), Early Miocene (Powell 1979, Eagle *et al.* 1994).

DESCRIPTION

Shell moderate size, ovate depressed; sculpture of imbricating strong radial folds crossed by spiral cords of three sizes; penultimate whorl of five well-defined, equispaced cords which increase in strength anteriorly, cover body-whorl; intermediate cords commence after first post-nuclear whorl, interspaces between main ribs with subsidiary median rib and finer rib either side also separated by interspaces; main spiral ribs 5 mm apart, radials likewise at middle of body-whorl; lower margin of shell keel spirally ribbed (number unknown due to matrix covering); protoconch worn, $\frac{1}{3}$ of length from left margin, less than $\frac{1}{3}$ width from front margin; tremata distinctly raised, tubular, numbering about 21 on body-whorl, five open. DIMENSIONS: Length 56 mm, width 46 mm, height (estimated) 17 mm.

REMARKS

Powell (1938: 377) considered *Haliotis* (*Notohaliotis*) *waitemataensis* to be undoubtedly of that subgenus, whilst declining to allocate a subgenus to *H. flemingi* described in the same paper on the same page. Geiger & Groves (1999) thought the Oligocene *Haliotis* sp. of Beu *et al.* (1990) similar to *H. (Notohaliotis) waitemataensis*, with a strong resemblance to the Recent Australian species *H. (Padollus) scalaris emmae* Reeve, 1846 (Fig. 24). Whilst the shell outline and growth folds of *scalaris emmae* are similar, fewer spiral cords on the sutural ramp and scales developed at intersections of the spiral cords with axial plicae differentiate *H. (Notohaliotis?)* sp. from *H. (P.) scalaris emmae*. Irrespective of shell form, DNA investigation of the *Notohaliotis* type, *H. ruber* indicates assignment to *Padollus* (Lee & Vacquier 1995). This example illustrates the difficulty in assigning subgenera originally erected to classify Recent species on the basis of shell morphology, to fossil species.

***Haliotis (Notohaliotis?)* sp.**

MATERIAL

See Beu *et al.* (1990) for the description and illustrations of this Duntroonian or Waitakian, late Oligocene (Chattian) fossil from the Cookson Volcanics at a road cutting on the Inland Kaikoura Road near "The Whaleback", North Canterbury. Several specimens are known, including GS9883.

REMARKS

Beu *et al.* (1990: 154) described this specimen (without naming it), commenting "the new species is apparently closely related to *H. (Notohaliotis) waitemataensis* (Otaian, Kawau Island [Figs 22–23]), but differs in having fewer spiral cords on the sutural ramp, and in having spines or scales developed at intersections of spiral cords with axial plicae". They considered that "the subcentral apex, the prominent spiral and scaly sculpture and the large tremata differentiate this species from other New Zealand haliotids".

SUBGENUS: *Padollus* Montfort, 1810

Type species: *H. scalaris* Leach, 1814 (= *H. rubicundus* Gray, 1826 [non *Haliotis rubicunda* Roding, 1798]; = *tricastalis* Menke, 1843; = *Neohaliotis* Cotton & Godfrey, 1933). Australia, Indo-Pacific, South Africa.

New Zealand species: *H. matihetihensis* Eagle, 1999, *H. australis* Gmelin, 1791.

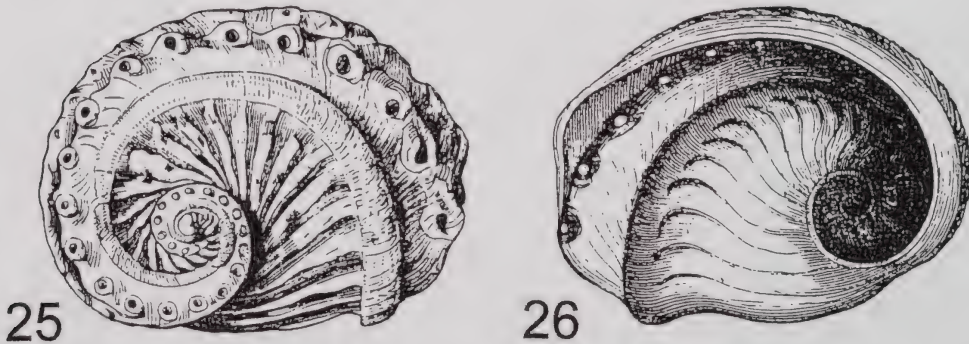
DIAGNOSIS

Broad spiral rib sometimes with prominent thin collabral lamellae on abapical side, or spiral striae sometimes crossed by irregular transverse ridges or nodes; tremata on low tubular projections at angulation separating upper whorl surface from concave outer face, commonly without frilly projections near periphery.

COMMENTS

H. (Padollus) scalaris (Figs 25, 26), a common Recent Western Australian species, is an ovate, thin-shelled haliotid with a moderately elevated spire. It is complexly sculptured with a thick central rib itself having scaly spiral cords, and it possesses thin, obliquely-inclined radial lamellae between the rib and the spire. The outer side of *H. (P.) scalaris* has a deep furrow between tremata of conical tubercles with moderately sized apertures (4–6 open) and a roughly nodulose marginal rib. Wilson *et al.* (1993: 50) considered *H. (P.) scalaris* and *H. (P.) emmae* (Fig. 24) to be "... obviously related. Specimens of *H. emmae* from western South Australia are intermediate in sculpture". This form of *H. (P.) scalaris* has since been synonymised with *H. (P.) emmae*, the latter becoming the subspecies *H. (P.) scalaris emmae* (e.g. Geiger 1999).

H. australis and *H. virginea* were assigned by conchologists on the basis of shell morphology to *Sulculus* (e.g. Powell 1979). However, *Sulculus* was originally diagnosed as a subgenus of *Padollus* and synonymised with the latter by most reviewers (e.g. Fleming 1952). Spencer & Willan (1995) in their review of New Zealand Mollusca continued to assign *H. australis* and *H. virginea* to *Sulculus*. Lee & Vacquier (1995) assigned the living New Zealand species *australis* to *Padollus* and *virginia* to *Paua*, replacing *Sulculus*. *H. matihetihensis* was incorrectly assigned by Eagle (1999) to the subgenus *Marinauris*; the juvenile specimen has a worn, raised, broadly rounded, prominent dorsal rib on the abapical side of the tremata with an apparently corresponding groove on the interior of the shell that are diagnostic of *Padollus*.



Figs 25–26. *Haliotis (Padollus) scalaris scalaris* (after Van Nostrand 1956). Length 66 mm. 25. Dorsal. 26. Ventral.

Haliotis (Padollus) matihetihensis Eagle, 1999

See Eagle (1999) for the description and illustrations of this Otaian (Aquitanian) fossil from the Waititi Formation, Otatau Group, north-west Hokianga, Northland. The holotype (AK73135) is the only specimen known.

REMARKS

Padollus is a more appropriate subgeneric assignment for *H. matihetihensis* because the shell is roundly ovate, the apex is not strongly eccentric, and a broad rounded spiral rib is prominent on the abapical side of the tremata. The tremata of *H. (Padollus) matihetihensis* are proportionately large on tubular, conical projections on (not 'adjacent to' as in the original description) a subdued second rib. The small size of the unique specimen suggests a juvenile, but the number of tremata and a reconstructed basal flange and apertural lip, suggest a sub-adult or adult specimen.

Haliotis (Padollus) australis Gmelin, 1791

(Figs 27, 28)

MATERIAL

GS15119, R28/f62, Cape Turakirae, Wellington (few fragments; 1855 uplift); GS12254, CH/f532, Okawa Point Formation, Owenga, Chatham Islands. (List provided by A. Beu, 23 April 2002.)

AGE

Holocene – Recent.

DESCRIPTION

Medium sized elongate-ovate *Haliotis*; spire of $2\frac{1}{2}$ whorls, elevated above sutural ramp; surface ornament of 10–15 densely spaced spiral striae of similar thickness and strength crossed by rough, irregular, transverse corrugations; tremata low, prominent, with orifices subcircular, usually 7–8 open; outer face with three prominent spiral ribs; rounded instead of flanged columellar margin; pale silver nacreous interior. DIMENSIONS: Length 107 mm, width 73 mm (average specimen).

REMARKS

A phylogenetic tree based on lysin cDNA by Lee & Vacquier (1995) grouped extant *H. australis* with the Australian Recent species *H. varia*, *H. ovina*, and *H. diversicolor* in the subgenus *Padollus*. The short, late fossil record suggests a moderately young species that has locally radiated sometime in the Pliocene-Pleistocene, possibly (by DNA inference) from Australian stock.

SUBGENUS: *Paua* Fleming, 1952

Type species: *Haliotis iris* Gmelin, 1791 (p. 3691; by subsequent description). New Zealand.

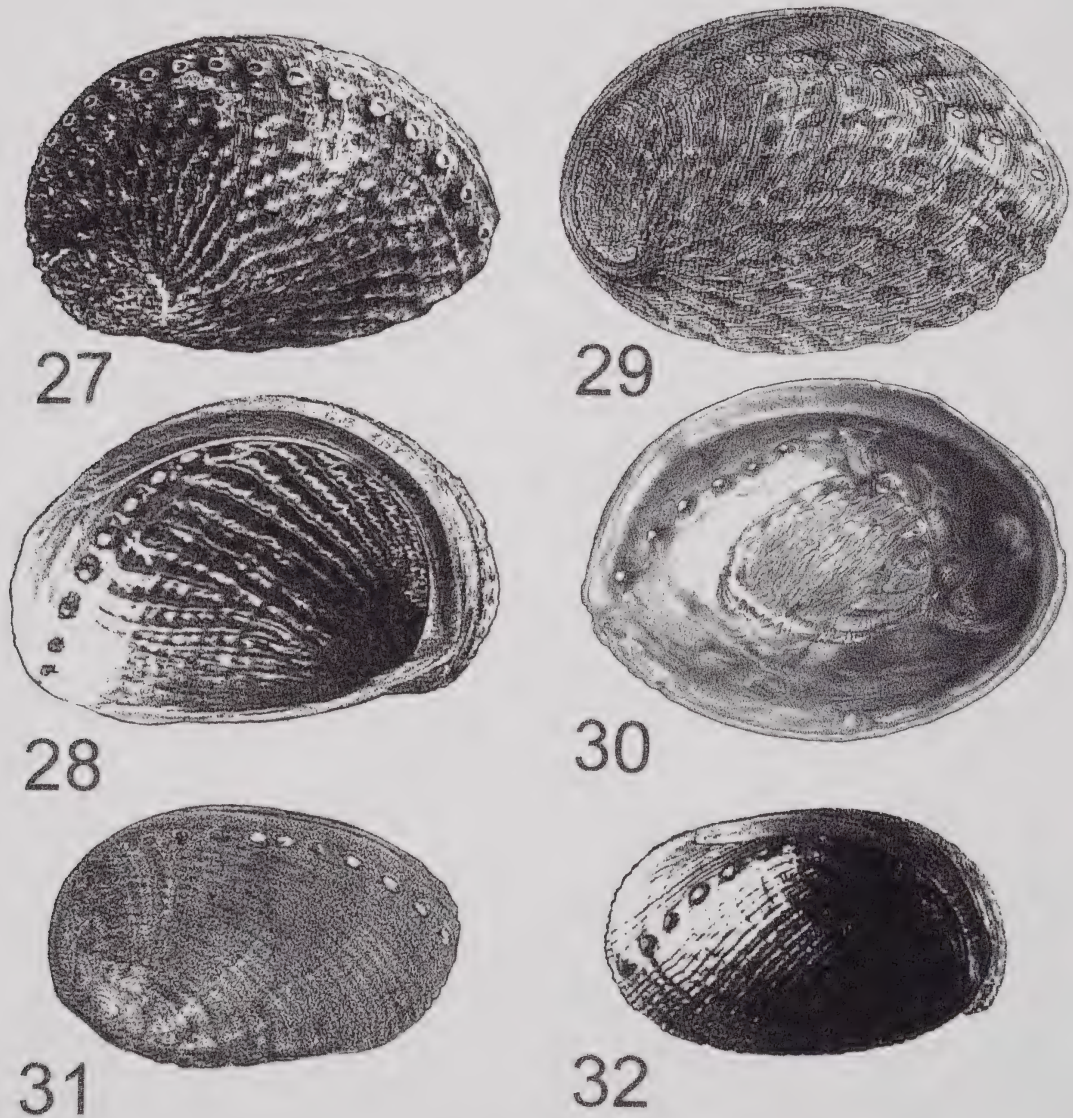
New Zealand species: *H. iris* Gmelin, 1791; *H. virginea* Gmelin, 1791; *H. flemingi* Powell, 1938.

DIAGNOSIS

Shell very large and solid, broadly ovate in outline with a wide, flat columellar flange continued below spire, meeting outer lip; whorls very rapidly increasing, profile slopes outward to columellar flange, forming periphery; spire filled with callus.

COMMENTS

The subgenus was erected by Fleming (1952) specifically to accommodate the shell morphology of *H. iris*. The phylogeny of lysin cDNA (Lee & Vacquier 1995) supports *Paua* as a valid subgenus.



Figs. 27–32. 27–28. *Haliotis (Padollus) australis*. Length 53 mm. 27. Dorsal. 28. Ventral. 29–30. *Haliotis (Paua) iris* (from Suter 1913). Length 102 mm. 29. Dorsal. 30. Ventral. 31–32. *Haliotis (Paua) virinea*. Length 41 mm. 31. Dorsal. 32. Ventral.

***Haliotis (Paua) iris* Gmelin, 1791**
(Figs 29, 30)

MATERIAL

GS996, R13/f6009, Kaawa Creek, Waikato (Opoitian; single complete shell). GS12482, U21/f10, Jumped-up Stream, Mangleton Road, inland central Hawke's Bay (Mangapanian; single incomplete shell). GS12681, E38/f19, Teer Formation, north coast Cascade Point, South Westland (Castlecliffian; fragments). GS1512, Y19/f9499, "raised beach" Te Mahanga, Mahia Peninsula (Holocene; single complete shell). GS15080, Y19/f65, marine terrace, Table Cape, Mahia Peninsula (Holocene; single small complete shell). GS6481, W21/f8556, GS13937, W21/f58, terrace in front of shelter hut, Cape Kidnappers (Holocene – 2.5 ka; small complete shells and fragments). GS15119, R28/f62, GS15121, R28/f72, Cape Turakirae, Wellington (Holocene – 1885 uplift; abundant complete shells). (List provided by A. Beu, 23 April 2002.)

AGE

Opoitian – Recent.

DESCRIPTION

Shell very large, thick, broadly-ovate; spire low, posteriorly fused with columella border with deep furrow between spire and border; teleconch of about $1\frac{1}{2}$ whorls, whorls very rapidly increasing; sutural ramp convex, sides rounded, sloping; basal columellar flange substantial, wide; spiral sculpture of broad spiral ribs at lower margin crossed by fine, axial growth ridges; tremata moderate-sized, low, nearly circular, apertures 3–4 mm diameter, 6–7 open, sited on angulation of dorsal margin; iridescent, nacreous interior; green-brown exterior. DIMENSIONS: Length 170 mm, width 128 mm, height 55 mm.

REMARKS

DNA inference suggests that *H. (Paua) iris* is a long-ranging taxon (Lee & Vacquier 1995), yet the species is known only from the Pliocene onward (A. Beu pers. comm., 23 April 2002). Migration, past climate/sea changes, lack of suitable facies, and preservation constraints may have all contributed to the brevity of the species in the New Zealand fossil record.

***Haliotis (Paua) virginea* Gmelin, 1791**
(Figs 31, 32)

MATERIAL

GS9323, O32/f8615, North Canterbury coast, stream south of Medina River, south of Conway (Nukumaruan). GS15037, T24/f127, shelly conglomerate, stream north of Saddle Road, north of Manawatu Gorge (Nukumaruan; single incomplete shell). GS12293, E38/f13, Teer Formation, north coast of Cascade Point, South Westland (Castlecliffian; shell fragments). GS4174, Q22/f7464, Oturi Shellbed, "Waipipi Beach", mouth of Wairoa Stream, Waverley Beach, west of Wanganui (Haweran – oxygen isotope 5c; single specimen). GS689, Y19/f9491, "raised beach" north shore Mahia Peninsula (Holocene). (List provided by A. Beu, 23 April 2002.)

AGE

Nukumaruan – Recent.

DESCRIPTION

Shell small, narrowly ovate; spire in adults enucleated in overall shape, prominent towards external lip; dense but rather weak external sculpture of narrow striae, crossed on the early whorls only, by weak axial corrugations, themselves forming weakly beaded striae; ornamentation extends beyond suture line onto upper outer face above columellar border; columellar border has slight furrow along entire length; interior highly iridescent, nacreous; exterior light brown, variegated with green.

REMARKS

Based on sperm lysin cDNA Lee & Vacquier (1995) suggested that *H. virginea* was a plausible inclusion with *H. iris* in the subgenus *Paua*. *H. (Paua) virginea* does not fit well with Fleming's (1952) diagnosis of *Paua. H. (P.) virginea*, is a much smaller, shorter, thinner shelled, and more inflated species than *H. (P.) iris*. However, *H. (P.) virginea* is as proportionately 'robust' as *H. (P.) iris*, is broadly ovate in outline, and has a flat columellar flange continued below the spire meeting the outer lip. Whorls of *H. (P.) virginea* do not increase as rapidly as those in *H. (P.) iris*, the spire is not as callused, and the shell profile does not slope outward to the columellar flange to the same degree. Fleming (1952) acknowledged the discrepant coiling in *H. (P.) virginea*. Range and exposure of *H. (P.) virginea* and *H. (P.) iris* are similar, but the latter's sub-littoral habitat, beneath shoreline boulders and on clean shell hash or gravel, is a more open environment. *H. (P.) virginea* and *H. (P.) iris* have different feeding niches. The larger and more abundant species lives mostly under ledges, in channels, and within sub-tidal caverns. *H. (P.) virginea* appears resident in New Zealand from at least the Nukumaruan onward. Poor preservation or lack of suitable bio-facies may have precluded collection of older material.

***Haliotis (Paua) flemingi* Powell, 1938**
(Figs 33, 34)

MATERIAL

Holotype. AK70349, complete specimen with some adherent matrix.

TYPE LOCALITY

Bostaquet Member, Cape Rodney Formation, Kawau Subgroup (Hayward & Brook 1984), basal Waitemata Group (Ballance 1974), Akarana Supergroup (Ballance *et al.* 1978); in sandy limestone, Fossil Point, east side of Bostaquet Bay, Kawau Island.

AGE

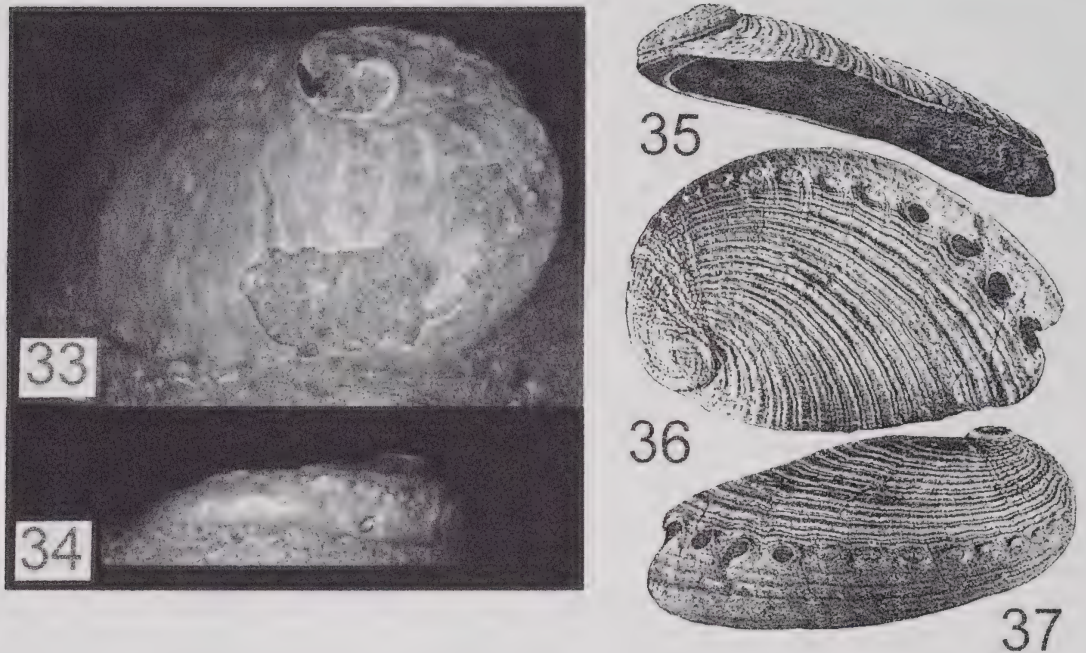
Early Otaian (Burgidalian), Early Miocene (Eagle *et al.* 1994).

DESCRIPTION

Shell moderate size, ovate, depressed; sculpturing irregular, arcuate, forwardly-directed radial folds, without spiral sculpture; 14 radial folds on last whorl; nucleus at about $\frac{1}{3}$ of length from left margin (allowance made for slight distortion); tremata slightly raised, 14 on last half-whorl; space smooth between tremata; space smooth on lower margin of shell. DIMENSIONS: Length 78 mm, width 55 mm, height (estimated) 19 mm.

REMARKS

Powell (1938: 377) wrote, "this species is ancestral to the Recent *australis* Gmelin, from which it differs in the absence of spiral sculpture, fewer radials, and the nucleus being nearer the



Figs 33–37. 33–34. Holotype of *Haliotis (Paua) flemingi* (AK70349). Length 78 mm. 33. Dorsal. 34. Posterior. 35–37. Holotype of *Haliotis (Sulculus) powelli* (GS3893.1; from Fleming 1952). Length 47 mm. 35. Anterior. 36. Dorsal. 37. Posterior.

middle”. Powell’s description of *H. flemingi* is diagnostic of the subgenus *Paua* (Eagle 1996, 1999), and not *Sulculus* to which it was assigned by Beu *et al.* (1990: 402). Beu *et al.* (1990: 347) state that “*H. flemingi* is much flatter and more prominently sculptured” than the Haweran to Recent *H. (Padollus) australis* and *H. (Paua) virginea*. Powell differentiated the Recent *H. (Padollus) australis* from the fossil *H. (Paua) flemingi* on the basis of shell morphology. Beu *et al.* (1990: 347) consider *H. (Paua) flemingi* as being “more coarsely sculptured, and with a narrower columellar lip than *H. (Paua) iris*”. Because *H. (Paua) flemingi* exhibits shell characteristics similar to that of *H. (Paua) iris*, it is more likely an ancestor to that species.

SUBGENUS *Sulculus* Adams & Adams, 1854
 Type species: *Haliotis incisa* Reeve, 1846 (by subsequent designation Crossmann, 1918). Recent, Japan.
 New Zealand species: *H. powelli* Fleming, 1952.

DIAGNOSIS

Small to medium-sized *Haliotis* with tremata on angulation separating upper whorl surface from concave outer face; sutural ramp ornament of spiral striae or cords with irregular transverse ridges or nodes.

COMMENTS

Fleming (1952) synonymised *Notohaliotis* and *Sanhaliotis* with *Sulculus* as Cotton (1943), in his review of Australian Haliotidae, had failed to indicate diagnostic differences amongst them

in his key. However, Knight *et al.* (1960: 1222) recognised “only one genus, divided into several more or less intergrading subgenera”, including *Sulculus*.

***Haliotis (Sulculus) powelli* Fleming, 1952**

(Figs 35–37)

MATERIAL

Holotype. GS3893.1, complete shell.

TYPE LOCALITY

W15/f7501, exposed face of sea cliff behind Ohope Beach, Whakatane, Bay of Plenty.

AGE

Castlecliffian.

DISTRIBUTION

There may be several undescribed New Zealand fossil haliotid species. Carter (1972) recorded a possible Nukumaruan occurrence of *Haliotis (Sulculus)* aff. *powelli* (OU7674) from N44/f565, Pohangina Valley, eastern Wanganui Basin. Lee *et al.* (1983) recorded an Oligocene *Haliotis* sp. from Mt. Luxmore, Fiordland, which may be *H. (S.) powelli*, or at least have affinities with it.

RANGE

?Oligocene – ?Nukumaruan – Castlecliffian (Putikian Substage) (Carter 1972, Lee *et al.* 1983, Beu *et al.* 1990).

DESCRIPTION

Shell small, elongate-oval, weakly inflated; low spiral apex; large, medially depressed last whorl with shallow spiral area between tremata and suture; large aperture; four open tremata low toward columellar lip; sealed tremata form a spiral row of low nodes; outer lip sinuous with median concavity corresponding with depressed area, rising steeply outside marginal tremata; inner and outer lips arched gently above basal horizontal plane; sutural ramp ornament of 21 prominent, narrow, rounded spiral costae, interspaced with several finer lirae crossed by irregular, weak to prominent growth ridges; periphery angled with sharp spiral cord with second cord between periphery and outer edge of columella, an additional three unevenly spaced rounded cords in a shallow depression between periphery and perforations. DIMENSIONS: Length 47 mm, width 30.5 mm, height 8.2 mm.

REMARKS

The small sized *H. (Sulculus) powelli*, was assigned to *Sulculus* by Fleming (1952: 230), on the basis that the subgenus “must apply to shells grouped around the type species, *incisa*, and not to shells agreeing with H. & A. Adams’ diagnosis”. He thought *Sulculus* to be the earliest name for small oval *Haliotis* with the pillar coiled in an open spiral, sculptured by spiral cords, crossed by growth-lamellae or radial ribs in some species, with an eccentric nucleus, lacking the characteristic dorsal fold of *Padollus* and its allies. Shell ornamentation and trematal orifice size is similar to *Marinauris*, but *H. (Sulculus) powelli* has only four open tremata instead of six (sited on low, not conical tremata), the labial area forms a projecting flange, and a strongly eccentric nucleus; these characters prevent allocation to that subgenus.



Fig. 38. *Haliotis (Sulculus) aff. powelli* (from Carter 1972). Length 11 mm. Dorsal.

Geiger & Groves (1999: 885) thought that the *Haliotis* sp. recorded by Lee *et al.* (1983) corresponded “exactly to the type of *H. powelli* illustrated in Beu *et al.* (1990)”. In the appendix of that paper they list (p. 883) the Mt. Luxmore, Fiordland, specimen as Late Miocene, not Oligocene as correctly recorded in the references (p. 880). The Mt. Luxmore specimen is here considered to have affinities with *powelli*; further study may resolve whether it is con-specific with that species. *H. (Sulculus) aff. powelli* (Fig. 38) when compared to *H. (S.) powelli*, is not as elongate-oval, lacks a shallow spiral area between tremata and suture, has smaller tremata openings, and a sutural ramp ornament of 15 (not 21) rounded spiral cords. The Pohangina Valley specimen of *H. (Sulculus) aff. powelli*, unlike *H. (S.) powelli*, possesses three very broad cords evenly spaced from one another across the sutural ramp, interspaced with narrow spiral cords crossed by irregular weak to prominent, almost nodulose growth ridges.

Fleming (1952: 231) stated that, “of the species available for comparison, *H. (S.) powelli* is closest to *H. coccoradiata* Reeve (Recent, New South Wales, Victoria)”. Recent Australian *H. clathrata* Reeve, 1846 (Figs 20, 21) is also very similar in shell morphology to *H. (Sulculus) powelli*, suggesting perhaps hybridisation from an ancestral Australian species before the Pleistocene.

DISCUSSION

Beu *et al.* (1990: 154) record New Zealand fossil haliotids as “. . . ranging in age from Mangaorapan to Opoitian . . .” (late-early Eocene to early Pliocene). Pleistocene and Holocene *Haliotis* specimens also occur. The fossil record suggests that New Zealand fossil, as well as Recent *Haliotis* species, are endemic, possibly the result of a long period of geographic isolation. Recent *Haliotis* planktonic larval stages vary with species (80–100+ days). Given ideal conditions, *Haliotis* should be able to migrate/colonise over great distances. Environmental factors may limit distribution, since this is not so for New Zealand.

Ten New Zealand fossil *Haliotis* species are allocated to six subgenera with few apparent lineages. Compared to the New Zealand fossil fauna, *Haliotis (Padollus) mooraboolensis* McCoy, 1876 from the late Miocene of Flemington, Victoria, Australia, is most similar to

H. (P.) matihetihensis, but different in having prominent, evenly spaced, low spiral ribs over the whole upper surface and a less depressed spire. The late Miocene-Pliocene Australian haliotid, *H. (Notohaliotis) naevosoides*, also from Flemington and elsewhere in Victoria, appears similar in overall shape and sculpture to *H. (Euhaliotis) mathesonensis*, but differs from that species in having a more eccentric, posteriorly sited spire, radial lirae oblique to collabral lines, less pronounced tremata, and no distinct, projecting notched labial flange. *H. (E.) mathesonensis* also appears similar to *H. (E.) midae* of South Africa. Another late Miocene haliotid from Victoria, Australia, *H. (Ovinotis) ovinoides* McCoy, 1876, is unlike any New Zealand fossil species, having tremata on large tubular projections, a knobby ornament on the sutural ramp, transverse ribs oblique to collabral lines, and obscure spiral threads. Lindberg (1992) recorded the extant Australian haliotid species *H. (Padollus; emend Lee & Vacquier 1995) cyclobates*, *H. (Padollus) emmae*, *H. (Padollus; emend Lee & Vacquier 1995) laevigata*, and *H. (Padollus; emend Lee & Vacquier 1995) ruber* as Pleistocene fossils from Victoria. Of these species, only *H. (P.) emmae* appears to have similar characteristics to a New Zealand fossil species, namely the early Miocene *H. (Notohaliotis) waitemataensis*.

Six New Zealand fossil haliotids are older than those presently known fossil from Australia, a situation possibly caused by the lack of suitable rocky shore facies there. The Australian late Miocene fossil *H. (Padollus) mooraboolensis* appears to have affinities with the New Zealand early Miocene species *H. (P.) matihetihensis*. The latter is also similar to the South African Recent species *H. (P.) parva* Linné, 1758. Several of the Recent Australian species have morphological characteristics similar to the older haliotids of New Zealand (e.g. *H. (Marinauris) ethologus* and *H. (M.) hokiangaensis*), and the New Zealand extant species *H. (Padollus) australis* has shell characteristics similar to those of the Recent Australian species *H. (P.) ruber*. The apparent incidence of New Zealand Cenozoic haliotids possessing shell characteristics of later Australian and South African taxa may be a result of convergent evolution in a local environment, but more likely a radiation eastwards from New Zealand in the late Oligocene onwards, when the circum-Antarctic Current began to flow and possibly distribute spawn.

In a cladistic analysis, Geiger (1999: 65) explained New Zealand's Recent endemic haliotid populations by suggesting "that these three species [*H. (Paua) iris*; *H. (Padollus) australis*; *H. (Paua) virginea*] seem to result from individual colonisations of the islands as contrasted with a small radiation in this rather isolated region. The basal split of *H. australis* from the remaining Australian species makes intuitive sense. The position of the other two taxa is more challenging to interpret". *H. (Paua) iris* would appear the oldest extant *Haliotis* species (Lee & Vacquier 1995; Geiger 1999) and with *H. (Paua) virginea* appear to have come from "some general south Indo-Pacific region". DNA inference in Recent New Zealand *Haliotis* suggests the possibility that in the late Palaeogene-early Neogene New Zealand haliotids were a result of local radiation from either ancestral Tethyan or Panthalassian Ocean progenitors. Subsequent geographic isolation and dispersal of New Zealand haliotids may have occurred in the fossil record at different times for different environmental reasons.

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